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THE ANNUAL ADDRESS OF THE PRESIDENT

THE THERMOCLINE AND ITS BIOLOGICAL SIGNIFICANCE

BY E. A. BIRGE

WITH TWO PLATES

It is my misfortune that my studies do not enable me to speak to this Society on a subject which is immediately connected with its name. To me, as to many biologists, the microscope has been an aid to work rather than an object of study in itself, and in preparing an address which shall deal with a topic of general scientific interest it has been necessary for me to select a subject which has but little direct relation to the microscope, although that instrument is the main aid to the student in working out the biological problems which the subject presents. However, it is not inappropriate that we should consider a topic relating to the biology of a lake when we meet, as we do to-day, on the shore of a sheet of water at once so beautiful and the subject of so much scientific investigation as is Winona Lake.

The term *thermocline* was introduced by myself in 1897, as an equivalent for the German term *Sprungschicht,* by which is meant that comparatively thin stratum in the water of a lake, situated below the surface, in which the temperature falls rapidly—much more rapidly than in strata of similar thickness above or below it.

It is a well known fact that in summer the temperature of a freshwater lake is much higher at the surface than at the bottom. The surface water may have a temperature anywhere from 20° to 30° C., while the bottom temperature varies in different lakes between 4° C. in deep bodies of water—the temperature of the maximum density of water—and a temperature very close to, or equal to that of the surface, in large and shallow lakes. Ordinarily, however, the difference is considerable. In small lakes, even though they are but 10 m. to 15 m. in depth, there is usually a temperature difference of 10° to 12° between the surface and the bottom.

When this fall of temperature is distributed to the several strata of the water between surface and bottom, it is seen that the decline is by no means uniform. Ordinarily there will be found a surface stratum of water, varying in different lakes from 2 m. to 12 m. in thickness, whose temperature is very nearly that of the surface. If at this season temperatures are taken in a lake like Winona in the early morning, before the sun has had an opportunity to warm the surface water, a stratum 5 m. to 6 m. in thickness may possess a temperature almost absolutely uniform. Immediately below this stratum comes another—the thermocline—in which the fall of temperature is very marked and very rapid. The temperature usually declines as much as 2° or 3° in the course of a meter and the fall may be much more rapid than this. A drop of 5° or 7°, or even 9° has been found in a single meter and in certain lakes a decline as great as 5° or 6° in the course of a meter may be ordinarily expected. This stratum, the thermocline, varies in thickness in different lakes and in the same lake under different circumstances, but may be from 2 m. or 3 m. to 5 m. in thickness. Its upper surface is pretty sharply marked and can usually be defined within the limits of a few decimeters. In its lower part, however, the thermocline passes more or less gradually into the region below and it is not possible to mark its lower surface by any exact level, though it is usually considered as ending where the decline in temperature becomes less than 1° per meter. Below the thermocline the rate of decline in temperature becomes rapidly smaller and soon amounts to only a few tenths of a degree per meter. As the depth increases the change in temperature becomes still less until perhaps, in the deepest lakes, the temperature of 4°, that of the maximum density of water, is reached, and below this point there is no further change.

This distribution of temperature in various lakes is illustrated by the following diagram (Plate I), which shows the distribution of temperature in three Wisconsin lakes on May 30 and September 2, 1898. These lakes are Garvin—a small pond having an area of about 8 hectares (20 acres) and a depth of about 11 m.; Okauchee Lake with an area of 4.4 sq. km. (1.7 sq. mi.) and a depth of 27 m.; and Lake Mendota, whose area is 39 sq. km. (15 sq. mi.) and whose depth is slightly over 24 m. These lakes are in the same general region; Garvin being immediately adjacent to Okauchee Lake, and both of these about 50 miles east of Lake Mendota. On May 30 Garvin Lake showed a strongly marked thermocline, whose upper surface lay at a depth of 4 m. and showed a fall of 7° in about half a meter. Okauchee Lake showed a thermocline extending from about 6 m. to 11 m., while Mendota on this date showed nothing that could fairly be called a thermocline. Thus the smallest lake showed a well-marked thermocline and the largest displayed a much more even distribution of the heat. The surface temperatures were lowest in Mendota and highest in Garvin. This would naturally follow from the greater influence of the wind in distributing the heat of the sun to greater depths in the larger lake. The bottom temperatures of the respective lakes showed the effect of the wind; Garvin at a depth of 11 m. being more than a degree lower than Okauchee at a depth of 27 m., while Lake Mendota, at a depth of 24 m., was nearly 2° higher than Okauchee Lake.

On September 2 all lakes showed well-marked thermoclines, which lay at a greater depth in the larger lakes. The variations in the surface temperatures on this day were due to the fact that the temperature of Lake Mendota was taken earlier in the morning, while the other lakes were visited later in the day; the temperature in Garvin Lake not being read until nearly noon. The bottom temperatures had increased comparatively little during the three months. Okauchee Lake indeed showed an apparent loss of 0.4°, which was probably due to an irregular stratification of the water on the earlier date. Garvin Lake at a depth of 11 m. had gained but half a degree, while Lake Mendota at the same depth had gained nearly 7°, and Okauchee about 1°.

This singular distribution of temperature was first noticed by Simony in Germany over fifty years ago. His observations were entirely forgotten and in 1885 Buchanan[1] observed the same phenomena in Loch Lomond, and Forel[2] about the same time in Lake Geneva. Their observations and explanations remained unnoticed and in 1891 Richter[3] gave new and careful investigation to the subject and applied the term *Sprungschicht* to the stratum of rapid change of temperature. His name for the stratum has been generally adopted, as also his explanation of the phenomena, although the latter is not wholly correct. Since this time the thermocline has been observed by all the very numerous students of lake temperature and much has been written regarding its nature and origin.

It is worth our while to spend a few minutes in considering the way in which the thermocline is formed, or rather, since the problem is really a more general one, to consider the explanation of the shape of the peculiar curve which represents the vertical distribution of temperature in a lake. (Plate II, fig. 2.) In all lakes of the northern United States, with which alone we are concerned, the temperature of the lake at freezing is but little above the temperature of 0° C. Ordinarily the bottom water, even in a lake 30 m. to 50 m. deep has a temperature of not more than 1° to 2°, and in lakes whose depth is 20 m., or more, it may easily be lower than 1°. During the winter the water under the ice is warmed, mainly by the action of the sun, and at the time of the melting of the ice in the spring the water has reached a temperature of 2° to 4° C., and usually is nearer the higher figure. When the ice has disappeared the water of the lake is freely exposed to the action of the weather. Practically all of the heat received by the water comes directly from the sun. Small amounts may be absorbed from the air and by reflection from the shores of the lake, but these are so insignificant in amount that they require no special consideration. The rays of the sun as they fall upon the lake are, in part, reflected; in part, used in evaporating the water of the surface; in very small part, employed for chemical operations in the plants and animals of the open water; and the remainder of the sun's energy, passing into the water, is there converted into heat. By far the greater portion of this energy is absorbed by the stratum of water immediately at the surface. Nearly one-half of the sun's energy is in the form of waves too long to be visible as light, and these are absorbed by the first centimeters of water through which they pass. Probably 30%, or more, of the energy present as light is absorbed by the first meter, so that even in distilled water not more than 30% to 35% of the energy which enters the surface of the water is transmitted to the second meter. In natural water, which is always rendered more or less turbid by the presence of suspended inorganic matter and of algae and plankton animals, the absorption is much greater, and in lakes whose water, when filtered, is clear and which are not at all exceptional in the amount of plankton which they may contain, only 3% or 4% of the sun's energy may be transmitted to the second meter; 95%, or more, being reflected or absorbed by the surface meter. If, therefore, the surface of the lake were not disturbed by the wind, the lower strata of water would be warmed during the course of the year very little, if at all. The surface strata would be greatly heated during the day; they would cool at night, to be again warmed as day returned, but the entire play of summer temperatures in the lake would take place in a shallow layer near the surface and the water at a very moderate depth would be slightly or not at all warmed above 4° C.

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[1] J. Y. Buchanan. On the distribution of temperature in Loch Lomond during the autumn of 1885. Proc. Royal Soc. Edin., Vol. XIII, 1886, pp. 403–428.

[2] F. A. Forel. Le Léman. Vol. II, p. 362, footnote.

[3] E. Richter. Die Temperaturverhältnisse der Alpenseen. Verhandl. d. neunten Geographentages zu Wein, 1891, pp. 176–189.

But the lake is exposed not only to the action of the sun, but to that of the wind, and the wind is the chief agent for the distribution through the body of water in the lake of the heat derived from the sun. This heat is distributed, in part, by the waves as they move, and especially as they break in whitecaps on the surface, but much more effectively by the currents which the wind causes on the surface of the lake.

Imagine a lake receiving no heat from the sun but exposed to the action of a wind which is blowing steadily in one direction. The surface water will not only be lifted into waves but will be driven by the wind across the lake. As it reaches the leeward side, it must return in some way, either around the edges of the lake, or across the bottom, and, since almost all lakes are very shallow in proportion to their breadth, a wind, such as is described, would finally set the entire mass of the water of the lake into a sort of rotation, completely mixing the surface and deeper water. Such a mixture as this actually occurs in late fall, after the lake has become homothermous. This is shown by the fact that even in lakes more than 70 m. in depth the temperature of the bottom water before the lake freezes falls below 4°, or the temperature of maximum density, and, further, during this period of cooling below 4° the difference of temperature between the surface and bottom water rarely exceeds 0.2° or 0.3° C.

If, however, the lake is exposed to the action of both sun and wind the influence of the wind becomes modified. The surface water, warmed by the sun, is driven across the lake but since the water becomes lighter as its temperature rises, there is produced a thermal resistance to the mixture of the water and the rotation described can not be set up unless the wind is very powerful. Instead of mingling with the lower water and returning easily by deep currents, the warmed water tends to remain on or near the surface and to accumulate on the leeward side of the lake. There is thus produced a sort of wedge-shaped layer of warm water, thickest on the leeward side and gradually tapering until it becomes very thin on the windward side. This wedge-shaped mass is, of course, in a condition of unstable equilibrium because of its shape and density. Equilibrium may be restored in various ways. The warmed water may, in small part, mingle with the cooler water by means of lateral diffusion currents. At night, as the temperature of the warmed surface falls, the thermal resistance to mixture declines and the task of the wind is rendered easier. On the cessation, or reversal, of the wind, the warmed water may flow back toward the leeward side, thus producing a surface layer of uniform thickness. If the wind is strong enough or if the action of the sun and wind continue long enough, the warmed water may flow back to the windward side along the shore, or beneath the surface and on top of the cooler water, thus producing a warmed surface layer of nearly uniform thickness. It is obvious that by one or all of these ways there could be produced on the surface of the cooler water of the lake a layer of warm water with a transition layer immediately below it—the thermocline.

If this were the entire story, the thermocline would be formed permanently very early in the spring and the bottom water would be only slightly warmed above 4°. But, as a matter of fact, while a warm surface layer is frequently produced during the day in spring, many days are so cool and cloudy that the small amount of heat gained is readily distributed to the depths of the lake. The long cool nights so reduce the surface temperature and diminish the thermal resistance to mixture that the winds may easily mix the surface water with all of that which lies below it. Almost always, too, during the spring there occur periods of cold weather and high winds, during which the entire stratum of warmed surface water will be cooled and mingled with the mass of the water of the lake. By these means the entire mass of the water of the lake may become warmed during the spring and the bottom temperature raised considerably above 4°. In Lake Mendota, whose area is 39 sq. km. (15 sq. mi.), the bottom temperature may rise to 10° or 12° at a depth of 24 meters. In Okauchee lake (4.4 sq. km.; 1.7 sq. mi.) the temperature at the same depth is 6° to 8°.

The distribution of the heat of the sun through the water of the lake is thus dependent on the mutual relation of two forces: first, the action of the wind, which tends by waves and currents to mingle the surface water with that which lies below it; and, second, the thermal resistance to mixture offered by the surface water as it is warmed. The influence of the wind is proportional to its velocity and duration. The thermal resistance is greater when the sun is shining; it is diminished at night, as the surface cools, and by cloudy or cold weather. The depth and extent to which the distribution of the warmth will take place depend on what may be called the algebraic sum of these two forces. The nocturnal cooling of the surface, and cooling due to periods of cloudy and cold weather are important aids to the distribution of heat, because they diminish the thermal resistance and thus give the wind an opportunity of mingling the water and so making the temperature of the lake more nearly uniform.

As the spring advances, the sun gets higher in the heavens, the days become longer and warmer, the nights shorter, and the influence of the sun upon the surface becomes greater. Under these circumstances there will come a time for each lake when even the strongest winds are unable completely to overcome the thermal resistance and when the action of the most violent and steady wind is able only to mingle the surface water with a small portion of that which lies below. Under these circumstances, a stratum will be formed on the surface nearly uniform in temperature and whose thickness will depend on the depth to which, under the prevailing temperature conditions, the ordinary winds are able to affect the water of the lake, especially at night, when the thermal resistance is least. Then the permanent thermocline will be formed and in the stratum above the thermocline the diurnal play of temperature will go on.

The result of this action is to divide the water of the lake into two main regions, with a transition zone between them. These are: first, a surface layer in which take place the diurnal changes of temperature—a stratum whose temperature is high and fairly uniform, though ordinarily declining somewhat below the surface; second, a transition stratum—the thermocline—in which the temperature falls rapidly to that of the cooler water of the lower part of the lake; and, third, below the thermocline and separated from it by no distinct line, lies the mass of the cooler water of the lake.

These thermal regions of the lake are very different in thickness in different lakes. In large and shallow lakes, indeed, there may be only one region, corresponding to the upper of the three regions named. In Wisconsin, for example, there is Lake Winnebago—a sheet of water more than 33 km. (20 mi.) in length, and perhaps 20 km. (12 mi.) in greatest width, with a maximum depth of 8 m. to 10 m. This body of water is so large and so shallow that the wind easily stirs it up to the bottom and the warmed surface strata are rapidly mingled with the entire mass of the water. As a result, the temperature of Lake Winnebago is odinarily uniform from top to bottom in the morning, although at night the surface strata will usually be warmer, unless the day has been very windy. In lakes which are in the same geographical region and whose depth in relation to area is of a more common type, the thickness of the warmed surface layer will vary with the area of the lake. In July the stratum may be as little as 2 m. or 3 m. in thickness in lakes whose area is from 8 to 10 hec. (20 to 30 acres). In lakes whose area is 3 or 4 sq. km. (one or more sq. mi.) the stratum may be from 5 m. to 7 m. in thickness. In lakes whose area is from 15 to 30 sq. km. the warmed stratum may be from 9 m. to 12 m. thick. In any case, it is true that the larger the lake the thicker the warm layer, or, in other words, the deeper lies the thermocline. This fact is a necessary result of the formation of the layer by the action of the wind, since in the larger body of water the wind has a greater opportunity to act upon the surface. It ought also to be said that the *effective* area of the lake should be considered, and the figures which I have given relate to lakes of fairly simple outline. A very irregular body of water, mainly consisting of narrow arms extending in various directions, would, of course, be much less influenced by the wind than a lake of simple outline. A similar statement might be made for a lake a large share of whose area is occupied by islands.

In different lakes the thermocline appears as a permanent feature at very different dates. In the smallest lakes—those in which the wind has the least effect—it no doubt may be permanent as early as the latter days of April, although I have never observed it earlier than the first week of May. In larger lakes it appears later, since the wind is able to mingle the surface water with the lower strata of the lake for a much longer time during the spring. In lakes whose area may be measured in square miles the thermocline is not likely to appear before the middle of June, and in Lake Mendota it can hardly be said to have a well-defined and permanent existence much before July. It should be noted, however, that it frequently appears temporarily at an earlier date and that the thermocline, in general, is by no means a phenomenon of late summer and autumn, as some of the earlier observers supposed. Other things being equal, the time of its appearance is conditioned upon the area of the lake—the date being earlier in the smaller body of water.

After the formation of the thermocline, the direct gains of heat are confined to the stratum of water above it. By this means the lower water is preserved in a cooler condition than would otherwise be the case. If the lake received its heat in smaller doses, as it were, such that the wind could mingle surface and deeper water, the temperature of the latter would rise far higher than it does. Okauchee Lake, for instance, has an area of about 4.4 sq. km. (1.72 sq. mi.) and a maximum depth of about 30 m. In 1898 the temperature of the water at the bottom had reached 6.5° by April 25; it was 7° on May 6; and after that date no perceptible rise was made until October. After the 1st of May the heat came so rapidly that the wind could not distribute it. Thus the lower water remained cool—much cooler than in a lake of larger area and equal depth. In small lakelets the sun produces little effect directly, even at depths which are very moderate. In one case the temperature at a depth of 11 m. rose only about 0.2° C. (4.33° to 4.55°) in 40 days, July 27 to September 5. A meter deeper no perceptible rise took place.

(Plate II, fig. 2.) The sun's effect is similarly confined to a small depth in the larger lakes, but the influence of the wind is so much greater as to prevent any direct proof of the fact by ordinary temperature observations. Thus a very low summer temperature may be maintained in comparatively shallow water if the area of the lake is small, and if it receives little or no ground water. It is obvious also that a cool spring, with its necessary alternations of warmth and cold, leads to the distribution of more heat to the lower water than does a warm season. Thus in Winona Lake in 1901 the bottom temperature was about 8°, while at the present time it is 2.5° higher.

It should also be added that the only periods when the entire mass of water in a lake is circulated freely are during late fall, after the lake has become homothermous, and the very brief period in the spring before the water reaches the temperature of 4° C. Thermal resistance prevents free circulation in the spring, and its effective opposition begins at a very early date.

By the first, or middle, of July, at latest, a warmed stratum has been formed on the surface of the lakes in this region of the United States and the thermocline is to be found at a depth which varies with the area of the lake but which is, in the same lake, about the same in successive years. For some weeks very little change occurs in the depth at which the thermocline lies. The surface of the lake is still gaining from the sun more heat than it radiates to the air, and the thermal resistance is such that it takes a very violent wind to mix the water to a depth greater than that at which the thermocline lies. Indeed, as one studies the temperature of the lake, he is surprised at the force of this thermal resistance. Squalls of very considerable violence and the strong winds which accompany summer showers, and which may last for many hours, may temporarily depress the thermocline on one side of a large lake perhaps 2 m. or 3 m., but they have very little effect in permanently lowering the thermocline, which rises almost to its former position when the wind ceases. One who follows the temperature of a lake with daily observations and notes the great oscillations of the upper surface of the thermocline and its very slow sinking in early and midsummer comes almost to feel that the upper surface of the thermocline offers such a resistance to the mixture of water as a thin elastic layer of rubber might do in the same position. In Okauchee Lake, for example, in 1898 the upper surface of the thermocline lay at 7 m. below the surface on June 28. Two and a half months later the upper surface was still at the same level, and the temperature of the upper stratum of water was not very different from that at the earlier date. In other lakes the same conditions are found. In Lake Mendota the upper surface of the thermocline at the middle of June, 1898, lay between 6 m. and 7 m. below the surface. Early in July it reached 8 m. and sank little more than a meter during July and August. In other years, as might be expected, the sinking is somewhat more rapid, but is always very slow during July and early August. In Garvin Lake, in the same year, the upper surface of the thermocline lay at 4 m. on June 28, and did not sink below that level in more than two months.

With the passing of the summer, as the nights increase in length and the gains from the sun become smaller, the thermal resistance to mixture decreases, and with the cool days and nights which often come in August and early September, there is brought about an equalizing of the temperature of the warmed layer. Under these circumstances, the wind more easily mingles this stratum and the upper part of the thermocline, and thus, as the temperature of the surface water falls, the thickness of the warmed layer increases, or, in other words, the position of the thermocline moves downward during the late summer and the early fall. As this process goes on, the thermocline is apt to sink with increasing rapidity, since the thermal difference between the upper and the lower water becomes smaller as the upper stratum cools, and the task of the wind, therefore, becomes easier. Usually the complete mingling of the water of the lakes comes in connection with a storm. In Lake Mendota, for instance, where most of my studies have been carried on, we have a lake about 10 km. (6 mi.) in length by 6.5 km. (4 mi.) in width, and with a maximum depth slightly exceeding 24 meters. The thermocline gets very near the bottom by the latter part of September, at which time the surface temperature may be about 18° and that of the bottom about 15°. Frequently the complete mixture of the water takes place during the gales which are wont to occur at the close of that month, or in early October. Should these not come, however, the equalizing of the temperature may not be brought about until late in October or in November. In smaller or deeper lakes the process of equalization lasts until later, and undoubtedly in the deepest lakes the homothermous condition is brought about more by the cooling of the surface water than by the overturning of the mass of water in the lake by the action of the wind.

This, then, is a brief sketch of the thermal history of any of our northern lakes. Starting in the spring, at a condition of thermal homogeneity, there is developed a condition by which the lake becomes separated into two very distinct thermal regions—a shallow, warm, surface layer resting on and ordinarily considerably thinner than the cooler bottom portion of the lake. These are connected by a transition stratum, the thermocline. During late summer and fall the warm layer loses heat and also gains in thickness by mixture with the subjacent water, until finally at some time during the autumn thermal homogeneity is reestablished.

These thermal changes must have a considerable effect on the physical conditions of life in a lake. The change of temperature at the thermocline is itself a factor which may influence directly the vertical distribution of life in a lake. Still further, change of temperature is accompanied with other physical changes. The cooler water is denser, and, therefore, plankton plants and animals may float in this denser water, which would sink in the warmer water above. Ostwald[1] has very recently pointed out that the viscosity of water increases as its temperature declines, and increases at a much more rapid rate than does its density. This increase of viscosity must affect the rate of sinking of plankton animals and plants, and so their vertical distribution. As yet, however, no experimental work in this direction has been published. Undoubtedly this newly suggested factor is a real one and its influence must be studied and evaluated. The initial influence of the viscosity of water is still unknown and it is, therefore, difficult to see how great the value of its increase will be. It appears also that it will not be easy to distinguish between the effects due to increased density and those due to increased viscosity.

Besides these more direct effects of the change in temperature at the thermocline, there are others less direct, but even more important in their influence on distribution. After the thermocline has been established, the water below is cut off from any direct access to the air. It is also deprived in great measure, though not entirely, of the effects which come from circulation induced by the wind.

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[1] W. Ostwald. Theoretische Planktonstudien. Zool. Jahrbücher, Abt. für Systematik, Vol. XVIII, 1903, pp. 1–62.

The movements of the warmed stratum occasion slow movements in the lower water, but these are very small and feeble as compared with the vigorous movements in the upper stratum. It is obvious also that the gaseous contents of the lower water are likely to become quite different from those of the upper stratum. All of the leaves blown into the lake, all organic debris washed into it, all of the plankton plants and animals, as they die, sink into the lower water and are there decomposed. Oxygen is consumed in this process and may almost entirely disappear from the lower water, as it is supplied only slowly to this water by diffusion from the upper stratum. The gases formed by decomposition escape also slowly, partly because of the lack of circulation, and partly because of the distance through which diffusion has to take place. The extent of this influence on gases and the substances dissolved in the lower water will depend on the amount of plankton or other organic matter present in the lake, on the volume of the water in the lower stratum, and on the temperature of the bottom water, which regulates the rate of decomposition. In large and deep lakes little, or no, influence of this kind can be detected. In small ponds, where the organic content is great and the bottom temperature high, the lower water may become very foul, ill-smelling, and discolored by the products of decomposition. All possible gradations between these extremes may be observed.

Another result of this thermal stratification of the lake is to produce like temperature conditions in the upper water of lakes in the same region, and so to render uniform the conditions of life near the surface. Very numerous observations have shown that lakes differing very greatly in area and depth and distant perhaps 100 miles from each other, differ no more in the temperature of their upper water than does the same lake at different times of the day. It might be thought that the warmed layer of the smaller lakes, being shallower, would be much more highly heated by the sun than is the thicker stratum of the larger lake. Yet this is not the case. The diurnal changes are somewhat greater in the smaller lake; and at noon of a hot day, with a slight breeze, the temperature of the surface in very small lakelets is higher than in the larger body of water. Yet a lake whose area is a sq. km. or even less has a surface temperature essentially the same, for biological purposes, as one of 50 times that area. There is then a general uniformity of temperature conditions at the surface. Different lakes in the same region differ far more widely in the thickness of the stratum above the thermocline than they do in its temperature, and for biological purposes, this stratum may be regarded as essentially identical. The temperature of the subthermocline in different lakes differs much more widely, as also does that of the water at the bottom.

During the summer, then, our typical northern lakes really consist of two lakes, one superposed on the other: first, the lake above the thermocline, whose temperature is high and whose water is kept in active movement by the wind; and below this, the stagnant mass of water below the thermocline, having a low temperature, denser and more viscous than the upper water, in which the gaseous and other products of decomposition are accumulating and from which they are only slowly and partially discharged.

Let us now turn from this general consideration of the physical conditions produced in the lake by the summer temperatures, and ask what effect this stratification of the water has upon the plants and animals of the plankton. We must say frankly at the outset that comparatively little is known in detail regarding this subject. As soon as investigation begins, it appears that we have not before us a simple problem which can be promptly solved, but that the question of the relation of the thermocline to life is one factor in the extremely complex subject of the vertical distribution of animal and vegetable plankton. What I have to say, therefore, will be much more in the way of suggestion than of presenting final results.

The following account of the biological influence of the thermocline on the vertical distribution of the plankton is based upon observations made upon lakes in Wisconsin. By far the most numerous and continuous observations were made upon Lake Mendota, which is immediately adjacent to the grounds of the University of Wisconsin. During the summer of 1898 observations were made about once in two weeks upon five smaller lakes in the Oconomowoc district, some 40 miles from Madison, and observations fewer in number, not exceeding two or three in a season, were made on more than 30 other lakes, chiefly in southern and central Wisconsin. The material from Lake Mendota comprises several hundred sets of observations. There are something more than 100 sets of observations from the other lakes. These, while sufficient to give a general idea of the vertical distribution of the animals and plants referred to, are not sufficient, except in Lake Mendota, to allow accurate conclusions to be drawn regarding the several species. My studies on Lake Mendota make it plain that in order to discuss the succession and distribution of forms in any lake with sufficient accuracy, it is necessary to follow them through at least one season with observations made as often as two or three times a week. This task, however, involves so great an amount of work that it is practically impossible to perform it for more than one or two lakes. The student must choose between obtaining a general view of many facts and an accurate knowledge of a few.

The relation of the thermocline to the vegetable plankton may be briefly stated. In general, the thermocline produces little direct effect upon vegetable life. The algae of the lake are so dependent upon sunlight that the greater part of the active vegetation is contained in the upper water which lies above the thermocline. Undoubtedly, the surface meter contains far more than its proportion of these algae. In lakes of considerable size, where the thermocline is 10 m., or more, below the surface, there would naturally be very little active plant development at its level. In the lakelets of small size, where the thermocline lies only 3 m. to 5 m. from the surface, the thinness of the stratum of warm water may exert an influence on the amount of algae in the lake and so on the amount of animal life which it can support. In lakes which are not peculiarly transparent green plants may grow from the bottom at a depth of 6 m., or more, and in lakes whose transparency is such that Secchi's disk can be seen to a depth of 5 m. to 6 m., there should be light enough to permit the active growth of algae at a depth of at least twice that distance. When, therefore, the temperature of the water at 6 m. or 7 m. is as low as 12° or 15°, there must be exerted an unfavorable influence on the total amount of vegetable life which the lake will support. So far as I know, however, no studies of this influence have been made, and it would probably be very difficult to distinguish this among the other, and mainly unknown, forces which make the difference between a lake rich in plankton and one containing little.

In another way, however, the thermocline has a very interesting relation to the algae. The fact is well known that in any lake the forms of algae appear in succession and each occupies the upper water almost to the exclusion of other species, then gradually passes away and its place is taken by another form. As any species of alga declines in number and dies out, it sinks gradually and it is found that under these circumstances the dying algae frequently accumulate in great numbers at the thermocline, so that at certain periods, lasting for as much as two days, the stratum included in the thermocline may contain a larger share of the alga-life of the lake than any other stratum of equal thickness. So far as my experience goes, this pausing of the sinking plants at the thermocline is more marked with the diatoms, such as *Fragilaria, Melosira,* and *Diatoma,* than with the blue-green algae. Botanists now tell us that the structures which keep these diatoms in suspension in the water are not certainly known. However this may be, it is clear that they are maintained in suspension by vital and not by mechanical means. They have none of the long spines which constitute the *Schwebeverrichtungen* of such genera as *Rhizosolenia* or *Atheya.* Those who have collected *Fragilaria* know that it very promptly settles to the bottom of a vessel when taken out from the lake, although it will remain for days, or even for weeks, suspended in the open water.

A moment's thought will show that the halting of these sinking algae at the thermocline is not a physical phenomenon, due to the decline of temperature and the increasing density of the water. If this were the case, the halting would only last long enough for the diatoms to acquire the temperature of the water, and, while their downward progress would be delayed, the halting would not extend beyond a very few minutes, although the sinking in the cooler water might be slower. Probably the cool water checks the progress of senescence and prolongs for a time the decaying life of the alga.

These diatoms are among the favorite food of the crustacea and indeed are preferred by most of the crustacea to the blue-green algae. At such times, therefore, as the successive crops of diatoms are found in the region of the thermocline, they are frequently accompanied by large numbers of crustacea, which then find more abundant, or more appetizing, food in that region than nearer the surface of the lake.

Under the conditions of plant life which have been thus described the number of algae found in the water of the subthermocline is ordinarily very small. This fact is not due to the distance from the surface and the consequent diminution of light, for the water close to the thermocline in Lake Mendota always has an abundant population of algae, which follows the thermocline downward as it descends and which in the autumn occupies the whole of the water, to the depth of 25 m., after it has become homothermous. In summer the algae, as they sink, seem to delay at the thermocline until they are dead, or so nearly dead that they fall rapidly to the bottom after passing that level. The crustacea which follow them to the thermocline do not go further with them; thus showing that other causes than lack of food prevent the occupation of the subthermocline by animals. Occasionally, therefore, large quantities of algae may be obtained from the lower water, with almost no crustacea or rotifers. Such periods are short and infrequent and usually the net brings up very little of either animal or vegetable life from this region.

In lakes whose lower water is habitable, the great masses of algae common in Lake Mendota are not often found. Yet the algae of such lakes also halt at the thermocline as they sink, and thus give occasion to accumulations of food at this point, and are probably one of the causes of the swarms of crustacea not infrequently found in that region.

In still another way, the thermocline may have an important indirect effect on vegetable life. Whipple[1] has pointed out that the products of decomposition, all of which accumulate in the subthermocline, constitute a sort of nutritive medium for the growth of algae, which can not be utilized because of the absence of sufficient light and warmth. As the thermocline moves downward, this nutritive material is distributed to the upper water, where it becomes available for plant food. He says also that when the thermocline disappears in the autumn and the water of the lake is "overturned" a large and sudden addition of plant food may be made, which will cause a great development of algae. He correlates with this overturning the appearance of large crops of algae in the autumn. This relation undoubtedly exists in the bodies of water which he observed, but in none of the lakes which I have studied is the accumulation of the products of decomposition anything like as great as that described by Whipple, and the addition of nutritive substances to the upper water by the overturning of the lake has not been great enough to produce any observable effects.

In addition to these relations of the thermocline to vegetation, the change of temperature at this level must also produce other effects. The increase in density of the water as its temperature declines must have an influence on the sinking of those algae whose specific gravity is only slightly greater than that of the warmer water in which they live. This is especially true of the blue-green algae, whose density during life hardly, if at all, exceeds that of the water. As these die and gradually sink, they must tend to linger at the thermocline, in consequence of the increased density of the water. The same effect must be produced by the increased viscosity of the water due to decreased temperature. Neither of these changes, however, appears to have any considerable influence on the rate of sinking of the ordinary plankton diatoms, whose specific gravity is considerably greater than that of water. Experiments show that they will pass in a very brief space of time an artificial thermocline considerably sharper than that in any lake. A greater effect may be produced on plants too small to be seen by the unassisted eye and these changes in density and viscosity may determine their position.

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[1] H. A. Whipple. The Temperature of Lakes. Trans. Am. Soc. Civil Engineers, 1895.

The relation of the thermocline to the vertical distribution of animal life is a far more complex matter than its relation to the algae. The change of temperature at this point may affect animals directly or indirectly. In the first case, the decline of temperature itself limits the downward movement of the plankton animals, or the rapid increase in warmth forms a barrier to their migration into the upper strata of the lake. Indirectly the change of temperature modifies the action of other forces, such as light, which are effective in determining the relation of the plankton animals to the surface. The stagnation of the lower water, which results from the thermocline, with the attending chemical changes, may also indirectly limit distribution. The increase in density and viscosity of the water, which accompanies the decline in temperature, will also exert an influence on the rate at which the plankton animals sink, and it may be found that these alterations are sufficient to permit animals to float at this level, which would sink in the warmer water above. This possibility holds especially for nauplii and other young forms. The adult crustacea and the rotifers which are large enough to be seen by the naked eye sink quite rapidly, both in the water above the thermocline and in the cooler water below.

It is not easy to trace any direct influence on vertical distribution of the change of temperature at the thermocline. Other factors than temperature are so much more important that the influence exerted by this one can hardly be detected and in few cases does it appear probable that temperature determines the position of animals. The best example of an animal whose position seems to be determined by the temperature of the water is furnished by the well known member of the Cladocera, *Diaphanosoma,* or *Daphnella.* This genus exists in two closely allied species; one inhabiting weedy water and marshes where the water is, of course, very warm; the other is limnetic in its habits. The latter species is more narrowly limited by temperature in its seasonal distribution than any other important member of the plankton crustacea. It appears later in the season and disappears earlier than any other form and while it is present, it is always confined to the region above the thermocline. Occasionally a few specimens may be captured from below the thermocline, but a large majority of such straggling individuals are diseased or have been unable to complete the shedding of the skin, or are in some way obviously disabled. Within the warm water above the thermocline the distribution of these animals is determined by various factors, which need not be discussed. The species differs so widely from other genera of plankton crustacea in never seeking the cooler water below the thermocline that it is not unfair to conclude that temperature is the most important factor in confining it to the superthermocline. It must be granted that light may also have its influence, but, as *Diaphanosoma* reacts negatively to a very bright light, and as the species occupies the whole of the warm water, whether 4 m. or 12 m. in thickness, the lower limit of its distribution seems to be set primarily by temperature.

There are two other forms of crustacea which it is possible may also be confined to the superthermocline for the same reason. There are *Ceriodaphnia lacustris* and the copepod *Epischura.* The former crustacean has been found only in the superthermocline but has appeared in small numbers and in few lakes, so that I hesitate to make any general proposition regarding it. *Epischura* was found only in the superthermocline of Green Lake by Marsh. I have never found it in sufficient numbers in other lakes to warrant any definite statement regarding its distribution. In Lake Mendota, where it has sometimes appeared in considerable numbers, it has ordinarily been found in the deeper water during the day, but this has been in the fall when the thermocline had moved far down. In Winona Lake it has been found to live in the thermocline by day and to move upward at night.

There is no rotifer which has been shown to be excluded from the thermocline by temperature. I am somewhat disposed to think that *Conochilus* may be such a form, but as I have found it in large numbers in Lake Mendota only, I can make no positive assertion, for reasons which follow.

The stagnation of the water below the thermocline, with the accompanying changes in its gaseous contents and dissolved matters, may become a very important factor in excluding the plankton animals from this region. Lake Mendota is an example of a lake whose subthermocline is almost uninhabitable. In that lake the entire mass of the water of the lake is freely occupied by crustacea and rotifers during April and May, and also late in the autumn. As the thermocline begins to be formed and the lower water becomes stagnant, the animals are gradually driven out of it, and after the early part of July the subthermocline is practically devoid of plankton animals. The few crustacea and rotifers which are found there are evidently diseased or feeble and are gradually sinking to the bottom. The suddenness with which the animal life disappears at the thermocline is very remarkable. I give a diagram (Plate II, fig. 1) showing the condition of the vertical distribution on September 8, 1896. At that date the thermocline began at 13 m.; at 12 m. nauplii were found at the rate of more than 220,000 per cubic meter; at 12.5 m. the number had fallen to 108,000; at 13 m., to 22,000; and at 13.5 m. and below, none were found. The adult crustacea ended with almost equal suddenness, though the absolute numbers were not nearly so great—something more than 10,000 per cu. m. being found at a depth of 12.5 m.; 2,000 at 13 m.; 400 at 13.5 m.; below which only an occasional straggler was found. Thus within the limits of a meter to a meter and a half at the thermocline the plankton population suddenly ceased.

It should be understood that this sharp limitation of the vertical distribution of the plankton animals is not due to the change of temperature at the thermocline. This fact is shown plainly by the relations in other lakes in which the vegetable plankton is less abundant, or the bottom water greater in quantity and colder, and in which the animals are freely distributed to all depths. It is the rule in the smaller lakes of Wisconsin that the animals occupy the whole mass of the water and only in three or four of the lakes has a relation been found similar to that in Lake Mendota. All of these lakes have abundant plankton and a comparatively small amount of water beneath the thermocline. They are of all sizes, however, the smallest being only 8 hectares (20 acres) in extent, and the largest 39 sq. km. (15 sq. mi.).

The subthermocline in these lakes is not entirely devoid of animal life. In Lake Mendota the mud is inhabited by *Cyclas,* and also by a few worms. These animals have not been found in the other lakes, where the conditions of bottom life are perhaps not as favorable as in Lake Mendota. The water of the subthermocline is inhabited by insect larvae, chiefly the larva of *Corethra.* This active and rapacious larva is well known to all students of fresh-water plankton as one of the largest, most transparent, and most beautiful of the creatures which the lakes contain. It is one of the animals which has a well-marked diurnal migration, moving down into the subthermocline during the day and passing the night in the warmer water above the thermocline. It will be remembered that the animal breathes by tracheae and that it contains two air sacs, so that even though the supply of oxygen in the subthermocline is deficient, it has no difficulty in remaining there for a considerable length of time. So far as my observation goes, it is most numerous in those lakes with abundant plankton and whose subthermocline is not inhabited by the crustacea and rotifers. In such lakes it not infrequently happens that the absolute number of *Corethra* larvae caught from the subthermocline exceeds that of the crustacea and rotifers together. Under these circumstances, it is evident that the larvae must do most of their feeding at night, since during the day there is hardly anything in the water surrounding them on which they can feed. It is probable that the action of light determines the position of these larvae, yet, although it is easy to understand the possibility of their passing the day in the water of the subthermocline, it is difficult to see why their habits should not have become adjusted to a continuous existence in the warmer water which they do not find uncomfortable at night, and in which their food is so much more plentiful than in the deeper water.

In lakes of the type of Lake Mendota only the upper water is occupied by plankton animals during the summer. In other words, of the two lakes into which the body of water is divided, only one is habitable. This fact exerts a considerable influence on the total quantity of animal life supported by the lake during the summer, as the number of animals is limited by the shallowness of the stratum to which they are confined. In each of the years during which the crustacea of Lake Mendota were studied, a midsummer minimum was found in the number of these animals. This was probably caused, in part, by the high temperature of the water, and, in part, by the exclusion of crustacea from the thermocline. Still further, the autumnal increase in the number of crustacea in this lake comes almost wholly from the progressive occupation of the lower water. As the thermocline moves downward, the population of the upper strata increases only very slightly, or, if any considerable temporary increase is found, it is due to the appearance of swarms of young, which live near the surface at their first appearance. The lower water, however, contains in the fall an abundance of algae in a healthy condition and supports a large population of plankton animals until the decrease of temperature in November causes a decline to their winter numbers.

We now turn from these lakes whose subthermocline is not habitable by the plankton animals, to those in which the lower water is abundantly supplied with oxygen and is, therefore, capable of supporting animal life. The first question which arises is the reverse of that which we have answered for the superthermocline; namely: are there animals which are confined to the subthermocline during summer because they are unable to endure the high temperature of the upper water? This is very probably the case with some of the crustacea found only in very deep lakes. In Green Lake, Wisconsin, which is more than 70 m. deep, there is an abyssal fauna, closely corresponding with the deep water fauna of Lake Michigan. It contains *Mysis* and *Pontoporeia,* the latter one of the amphipods. Whatever may be the cause which first drove these crustacea into the deeper water, it is certain that they always remain here, and, so far as is known, do not appear in the warmed surface water, either by day or by night. Besides these representatives of the higher crustacea, there is also found in the depth of the lake the copepod *Limnocalanus,* which, Marsh reports, is confined to the deep water during summer. The animal, however, has appeared in surface collections made by night in Lake Geneva, so that it is not absolutely confined to the subthermocline.

One member of the Cladocera has appeared only in collections from the bottom water of the lakes. This is *Daphnia longiremis*—a form belonging to the hyaline section of this genus and distinguished, as the name implies, by extremely long antennae. This species has been found in a few lakes only, whose waters are deep in proportion to their area and consequently are cold. In these lakes it was always found close to the bottom. It has never appeared in numbers throughout the subthermocline but has been aggregated within a few meters of the bottom and in largest numbers just above the mud. Its position here is very possibly determined by the presence of food and there is no reason to suppose that temperature alone determines its position. This species has never appeared at the surface in collections made by night, yet the observations on this subject have not been sufficiently numerous to warrant me in asserting positively that it never comes to the surface. We are, however, warranted in stating that, so far as is known, this is the only member of the common genera of plankton crustacea which, by preference, occupies a position at the bottom of the deeper lakes in the coldest water to be found—water whose temperature ranges from 6° to 8° C.

The most interesting of the animals found, by preference, in the subthermocline, is *Daphnia pulicaria.* This is a large, stout *Daphnia,* belonging to the *pulex* group. It is found in many lakes and during the summer is regularly an inhabitant of the subthermocline. It might be supposed that temperature immediately determined the position of this creature, yet such is not the case. The animal responds negatively to light, and this fact appears to determine its position in the lake, the lower temperature of the water of the thermocline being effective in lessening or reversing the negative action of the light. It is well known that many of the plankton animals respond negatively to light, moving downward in the water to varying distances according to their sensitiveness to this influence. This negative action of light is greatly increased as the water becomes higher in temperature and when the temperature of the water is lowered the animals may become indifferent to light, or may move toward a light which would repel them were the temperature higher. Such seems to be the case with *Daphnia pulicaria.* It is found at the surface in the spring and until the water reaches its summer temperature. It also has a period of active reproduction late in the autumn, when the water has cooled, and then occupies the water at the surface, as well as at all depths. In winter it may often be seen in great numbers immediately below the transparent ice. In summer, however, it moves downward below the thermocline and is found there alone, though occasionally a few straggling individuals may be captured in the warm water.

That the position of *Daphnia pulicaria* is determined by light rather than by temperature appears from the fact that in certain lakes it comes to the surface at night, moving upward into water often as much as 15° C. warmer than that which it occupies by day. This upward movement is probably in search of food and the absence of light is a condition and not a cause of the migration. The species has been found to appear at the surface about two hours after sunset and it disappears before sunrise, while the sky is still dark. If temperature alone determined its position in the subthermocline, it would not move upward into the warmer water at all.

While this species may be found throughout the subthermocline of the lakes which it inhabits, the largest numbers are wont to stay in the immediate neighborhood of the thermocline. This is probably due to the fact that this stratum contains a larger amount of food, for reasons which have already been stated, than does any other equally thick stratum of the lake below the surface. Possibly the action of the light becomes positive in the cooler water. Yet the animals are so generally distributed in the subthermocline as to render this hypothesis improbable. In Lake Mendota, whose subthermocline is not habitable by the plankton crustacea, *Daphnia pulicaria* is present and in summer is forced to occupy a very narrow space just at the thermocline. Almost all of the members of the species are ordinarily found in a stratum of water not much more than a meter thick, at the junction of the thermocline with the warmer water above; the temperature preventing it from rising into the warmer water, and the nature of the subthermocline making it impossible for the animal to descend into it. In this lake no vertical migration of the species at night has been detected.

When now we turn to the other species of crustacea and rotifers comprising the great mass of the plankton animals, we have to do with forms which are not confined to any one thermal region of the lake, and we can speak only of a preference for this or that region. We find also in different lakes and on different occasions in the same lake a varying distribution of the same species. It is evident that other factors than temperature are the principal forces which determine the vertical distribution. The most important of these factors are light and food, yet these affect different species in very different degrees and the thermocline has a marked influence on the distribution of most forms.

The two genera of Copepoda which contribute most to the plankton are *Cyclops* and *Diaptomus*. The former genus is more uniformly distributed through the water than any other of the plankton animals. It is comparatively indifferent to light, and temperature has no noticeable influence upon it. *Diaptomus* responds much more definitely to light and a larger proportion of individuals is usually found in the upper strata of water. In neither genus is any sharp break in distribution regularly made by the thermocline. At times there are found large aggregations of both of these genera at the thermocline. In some lakes *Diaptomus* seems to be driven by sunlight into the thermocline by day, rising into the warm water at night. The same statements may be made for the nauplii as for the adults of both these genera of Copepoda. In the illustration which I give of the distribution in September, the majority of the nauplii were aggregated just above the thermocline. I have never found these aggregations, which may be very great, elsewhere than at the surface and thermocline. In the case of the adult Copepoda, the swarms, as they become old, are wont to move downward in the lake and occasionally large numbers of adults are found close to the bottom. This is evidently the result of old age. The aggregations at the surface and thermocline are probably, although not certainly, due mainly to the food which is present at these places, either in large quantities or in forms which are especially desired. The surface meter and the thermocline are the two regions of the lake in which great crowds of plankton animals may be found, and it rarely happens that some species or other is not present in unusual numbers at the thermocline.

The member of the group of Cladocera which is universally present in the plankton is *Daphnia hyalina*. The distribution of this species corresponds very closely with that of *Diaptomus*. Like that genus, it is ordinarily most numerous in the upper water, but it is also true that large aggregations of the species may be found at the thermocline—a fact which again is probably attributable to food.

A large number of species of rotifers are, in like manner, distributed through the waters of the lakes; aggregated occasionally in great numbers at the thermocline, at the surface, or at the bottom, or again, more uniformly distributed through the entire depth of the water. Many more observations would be needed on these animals, as well as on the crustacea, in order to work out in detail the laws of their distribution. Yet so far as my observations extend, certain preferences in position are indicated. Among the common rotifers which are ordinarily, though not exclusively, found in the warm surface water of the lakes in summer are *Asplancha, Polyarthra, Conochilus, Mastigocerca,* and *Anuraea cochlearis.* Those found by preference in the cooler bottom water are *Anuraea aculeata* and *Notholca longispina.* In all of these rotifers the distribution was, in general, as indicated, yet not without exception. In several cases swarms were found at the bottom, even of the deepest lakes. Yet in these cases the animals were all adult and it appears probable that these constituted the last part of a generation-cycle. In all cases, too, there were found some exceptions to the general rule of distribution; the rotifers which ordinarily belong below the thermocline being above it in certain lakes, and *vice versa.* These exceptions, however, were few in number. In no case does it appear probable that the change in the temperature of the water constitutes in itself an important barrier to the movements of these animals. Yet we are also warranted in saying that the preference of one set of species is for the warmer water and of the other is for the cold. This is especially noticeable in the case of the closely allied species *Anuraea cochlearis* and *A. aculeata.* These are found in the same lakes and frequently in considerable numbers, although the former species is ordinarily by far the more abundant. In no case where the two species were found together was the arrangement other than that which was indicated; *A. cochlearis* occupying the upper water, although extending into the subthermocline; and the majority of the individuals of *A. aculeata* coming from below the thermocline.

From this account we may fairly infer that the thermocline constitutes a critical point in the distribution of the plankton in the water below the surface. No single factor within the water itself compares with it in importance. The direct influence of the change of temperature is not very great and in this respect the difference of temperature in the lake corresponds to temperature differences in general. Most plants and animals of temperate regions are not particularly sensitive to a change of a few degrees of temperature. For some species, however, the change from warm to cool water constitutes the factor which determines their vertical distribution. Indirectly, the effect of the thermocline is far greater. The stagnation of the lower water, with its attendant chemical results, causes a sharp limitation on the distribution of the animal life in many lakes. The thermocline in these lakes marks the limit of the thriving of algae and thus directly limits the distribution of plants and indirectly that of the animals which feed upon them. In all lakes the thermocline has an evident influence upon distribution, and, although it is by no means an impassable barrier, most species of plankton animals live, by preference, either above or below it. The fact that the thermocline is the one stratum below the surface where large numbers of the plankton animals are often aggregated is sufficient to indicate its importance.

The thermocline is, however, only one factor in the complex of forces which determine the position of plants and animals in the water of our lakes. Some of these, as light and food, density and viscosity, have been named, but these, with temperature, are not the only factors. Others, like gravitation, have an effect difficult to trace, but none the less real. Competing species and plants of the plankton which are not edible have an influence which the observer can feel but whose value he finds it even more difficult to estimate. Each of these forces is independent of the others, both in the direction and the intensity of its action. They differ in their effect on the individuals of different species and their influence on the same animal may change as it passes from youth to maturity and old age. Still more, these forces are affecting animals of highly complex organization, whose reactions are not always marked by the directness and uniformity of a unicellular animal.

Thus the problem of the vertical distribution of plankton animals becomes very complicated and requires for its full solution far more numerous and careful studies than those on which this address is based. It was an investigator and a lake of Indiana that suggested the phrase: " The lake as a unit of environment." The years which have passed since that phrase was uttered have shown, on the one hand, its essential truth, and, on the other, have partially revealed to the student of lake biology the great inner complexity of this unit, and the amount of research which its problems demand. This question of vertical distribution on which I have touched is among the simpler problems of the lake. Yet we have no accurate knowledge of the effects of any one of the factors which determine it, nor do we know how these factors influence any one species of the plankton. Here is a wide field open to the investigator. I say " open " because any student may work in it. Complicated apparatus and difficult processes are not demanded; at any rate, for the present. Patient and intelligent observation by day and night with pump, plankton net, and microscope, will be rewarded by large additions to knowledge. By these means we may hope to make a beginning in unraveling the tangled story of the interrelations of the inhabitants of this " unit of environment." We may hope thus to trace, in part, their relations to the lake in which they live and to the forces of the larger world which act on them with an apparent simplicity, all the more provoking as it masks a real complexity so great that the increase in our knowledge of the facts seems thus for to bring little more than increase in ignorance of principles. Each lake and lakelet, almost each species in each lake, seems thus far to be a peculiar case and to have its own singularities so marked that it is difficult, or impossible, to unite them in any general statement. Only a large body of most careful observations can furnish material which will show in what sense each lake is " a unit of invironment," and how each furnishes but a special case in the larger statement of the laws of lake biology.

PLATE I

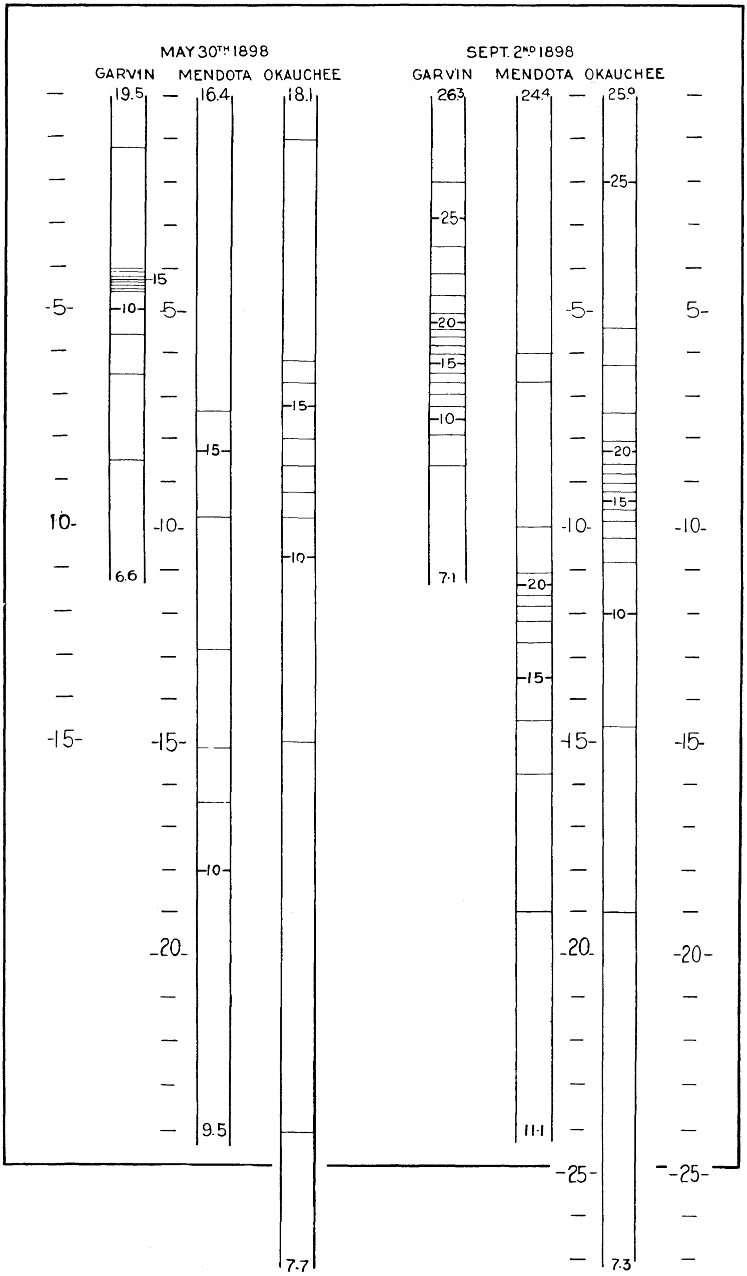
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PLATE II

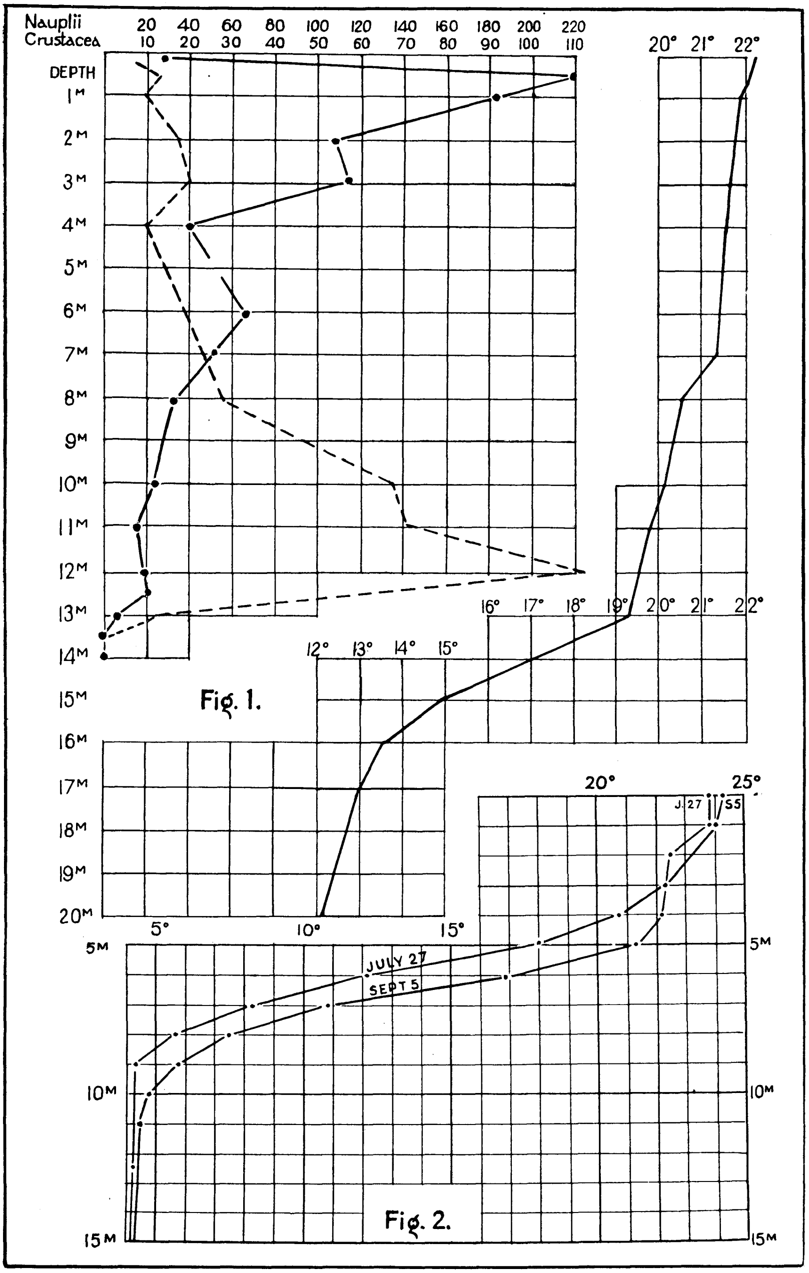

Fig. 1.

Fig. 2.

EXPLANATION OF PLATES

Plate I

Temperature diagrams of Lakes Garvin, Okauchee, and Mendota on May 30 and September 2, 1898. The depth is indicated by a scale placed beside the columns on which is platted the distribution of temperature. For further explanation see text.

Plate II

Fig. 1. Curves showing the vertical distribution of adult crustacea of all kinds, of copepod nauplii, and of temperature, in Lake Mendota September 8, 1896. Each space on the vertical scale indicates one meter in depth. On the horizontal scale each space represents 10,000 crustacea per cubic meter of water, or 20,000 nauplii per cubic meter, or 1° of temperature. The distribution of the crustacea was determined by the pump at the depths indicated by dots on the line representing the number of crustacea present. The numbers indicate the rate of the population of crustacea or nauplii at the depths indicated and not the number found between the successive levels of one meter. The temperature curve shows a slight surface warming, a secondary thermocline between 7 m. and 8 m. due to warm weather several days earlier, and the permanent thermocline beginning at the depth of 13 m.

Fig. 2. Temperature curves of Beasley Lake, Wisconsin, on July 27 and September 5, 1898. These curves show the amount of sinking of the thermocline during the 40 days between the dates named. They show also the very slight change in temperature below the depth of 11 m.